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Smallmouth Bass (*Micropterus dolomieu*) Invasion of Gulf Region Rivers: Evaluating the Impact on Atlantic Salmon (*Salmo salar*) Populations

Invasion des rivières de la région du Golfe par l'achigan à petite bouche (*Micropterus dolomieu*) : Évaluation des impacts sur les populations de saumon atlantique (*Salmo salar*)

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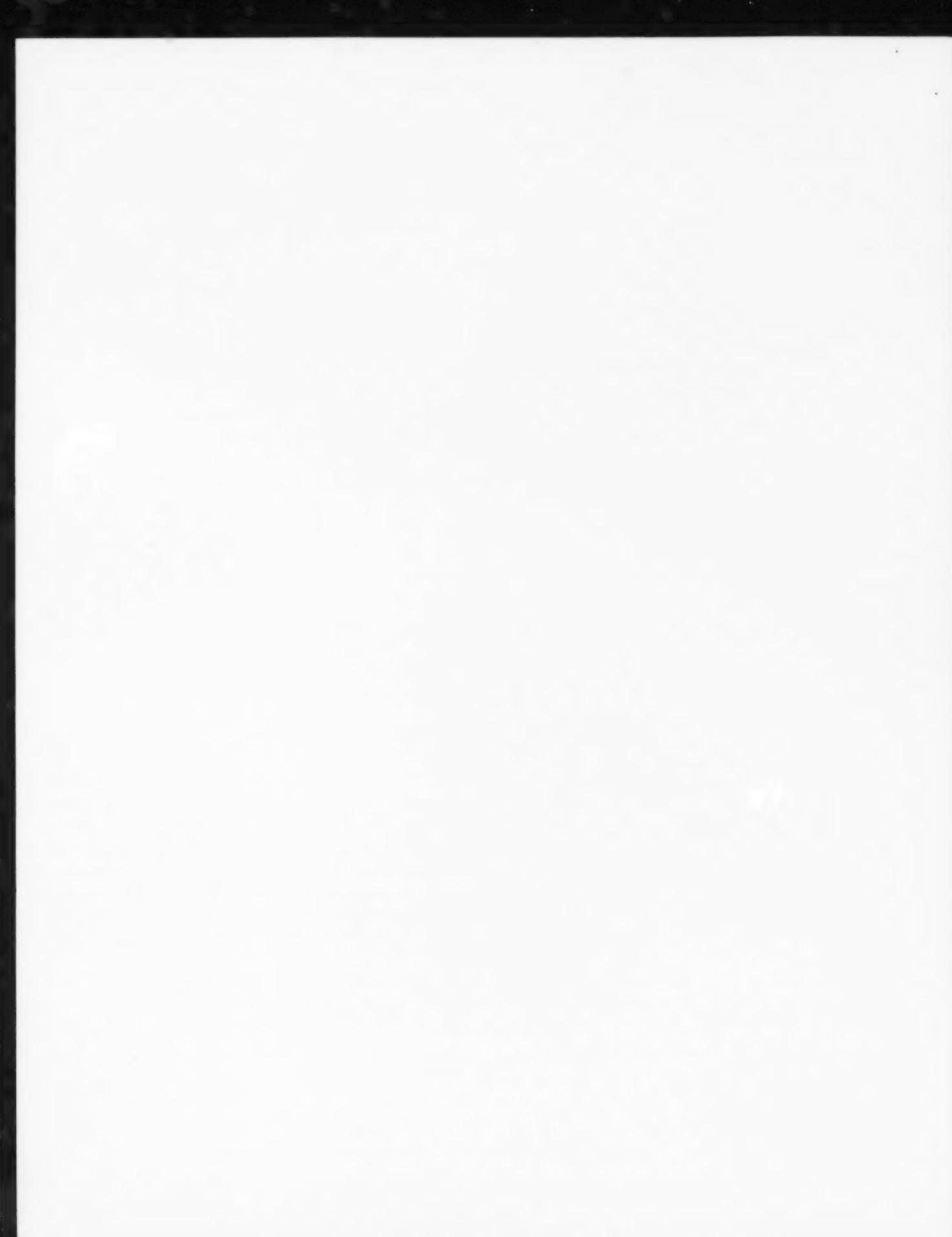


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ABSTRACT

The introduction of species outside their native range can lead to significant declines in native fish species, including Atlantic salmon (*Salmo salar*). The rapid natural and human-facilitated expansion of smallmouth bass (*Micropterus dolomieu*) throughout New England and the Maritimes has brought increased attention to possible negative effects of these introductions on efforts to maintain and restore Atlantic salmon. Although the negative effects of invasive smallmouth bass on other native fishes (e.g., cyprinids, Pacific salmonids) are well-documented, we have no direct studies assessing predatory and competitive interactions with Atlantic salmon. The predation risk leading to the most significant potential threat to Atlantic salmon will be consumption of juveniles, i.e., emerging fry to smolts. Smolts probably have lower risk of predation than younger parr owing to the larger body size of smolts. Studies of habitat use and foraging behaviour of juvenile smallmouth bass in streams suggest functional similarities and potential habitat overlap with Atlantic salmon that could result in competitive interactions with age 0+ smallmouth bass. These negative effects resultant from competition with smallmouth bass would be most pronounced during energetically-stressful summer periods of high water temperatures, reduced stream flows, and decreased prey availability. The effects of smallmouth bass on native fish species are most significant when systems are less biologically and physically complex. In most eastern rivers inhabited by Atlantic salmon, both conditions are common: there are few fish species, and, habitats for smallmouth bass would be slow, deeper waters. Consequently, a significant degree of interaction between Atlantic salmon and smallmouth bass is predicted to occur in eastern rivers.

RÉSUMÉ

L'introduction de l'espèce à l'extérieur de son aire de répartition naturelle peut entraîner d'importantes diminutions des espèces de poissons indigènes, notamment le saumon atlantique (*Salmo salar*). L'expansion rapide de l'achigan à petite bouche (*Micropterus dolomieu*), à la fois naturelle et facilitée par l'humain, partout en Nouvelle-Angleterre et dans les Maritimes, a attiré une attention accrue sur les possibles effets négatifs de telles introductions sur les efforts visant à maintenir et à rétablir le saumon atlantique. Bien que les effets négatifs de l'achigan à petite bouche envahissant les autres espèces de poissons indigènes (p. ex. cyprinidés, salmonidés du Pacifique) soient bien documentés, aucune étude directe n'évalue les interactions de prédation et de compétition avec le saumon atlantique. Le risque de prédation menant à la plus importante menace éventuelle pour le saumon atlantique est la consommation de juvéniles, c.-à-d. des nouveaux alevins aux saumoneaux. En raison de sa plus grande taille, le saumoneau est moins exposé à la prédation que le jeune tacon. Des études portant sur l'utilisation de l'habitat et le comportement en quête de nourriture des achigans à petite bouche juvéniles dans les cours d'eau laissent entrevoir des ressemblances fonctionnelles et un chevauchement potentiel de l'habitat avec le saumon atlantique, ce qui pourrait entraîner des interactions de compétition avec l'achigan à petite bouche d'âge 0 et plus. Ces effets négatifs découlant de la compétition avec l'achigan à petite bouche atteindront leur sommet lors des périodes estivales, qui demandent beaucoup d'énergie aux poissons, alors que la température de l'eau est élevée, que le débit est réduit et que la disponibilité des proies est réduite. Les effets de l'achigan à petite bouche sur les espèces de poissons indigènes sont plus marquants lorsque les systèmes sont moins complexes sur les plans biologique et physique. Dans la plupart des rivières de l'Est habitées par le saumon atlantique, les deux conditions sont communes : il y a moins d'espèces de poissons et l'habitat de l'achigan à petite bouche correspond aux eaux calmes et plus profondes. Par conséquent, on prévoit un niveau important d'interaction entre le saumon atlantique et l'achigan à petite bouche dans les rivières de l'Est.

1.0 INTRODUCTION

The rapid natural and human-facilitated spread of smallmouth bass (*Micropterus dolomieu*) throughout New England and the Maritimes has brought increased attention to possible negative consequences of these introductions on efforts to maintain and restore Atlantic salmon (*Salmo salar*). Linking declines in Atlantic salmon populations with the spread of invasive species is difficult considering the multitude of factors operating in riverine and marine environments that are known to influence the survival of Atlantic salmon. Evidence of the effects of smallmouth bass introductions on Atlantic salmon has recently emerged (van den Ende 1993). On the west coast, production of Pacific salmon (*Oncorhynchus* spp.) can be reduced in response to the introduction of warm-water species. For example, introduced largemouth bass (*Micropterus salmoides*) and walleye (*Sander vitreus*) consume and thus increase mortality rates for juvenile Pacific salmon (McMahon and Bennett 1996; Bonar et al. 2005). In 2008, smallmouth bass were reported in the Miramichi River system which is one of the most productive Atlantic salmon rivers in the world and with a local culture and economy closely linked to the salmon fishery. In response to this discovery, Fisheries and Oceans Canada (DFO) initiated a science review to determine the potential impact of smallmouth bass on salmonids in Gulf Region rivers.

2.0 SMALLMOUTH BASS

2.1 Distribution and Range Expansion

Smallmouth bass are native to the Mississippi River and the Great Lakes watershed in central North America. Their natural range extends from Minnesota eastward to Quebec and south to Northern Alabama (Scott and Crossman 1973). The Appalachian Mountains formed a barrier to the northeast which prevented their expansion into New England, Maine and the Maritime provinces (MacCrimmon and Robbins 1975; Lee et al. 1980; Curry 2007). They were introduced into Maine in 1868 (Foster and Atkins 1869) and subsequently into southwestern New Brunswick (Catt 1949) where they have become naturalized. Smallmouth bass were introduced initially into the St. Croix River and are now found throughout the Saint John, Magaguadavic, Musquash, Petitcodiac, Kennebecasis and St. Croix rivers (M. Sabine, NB Department of Natural Resources, unpublished data). Smallmouth bass were introduced into Yarmouth County (Nova Scotia) in 1942, with new introductions occurring in Nova Scotia as recently as 1984 (McNeil 1995). Although smallmouth bass are no longer stocked in new lakes in the Maritimes (NB, NS and PEI), their northward expansion continues through natural dispersal along waterways and by illegal introductions by humans. Most recently, smallmouth bass have been found in Miramichi Lake which drains into a headwater tributary of the Southwest Miramichi River. This is the first report of the presence of smallmouth bass in the Miramichi River watershed (M. Sabine, NB Department of Natural Resources, pers. comm.).

2.2 Life History

Smallmouth bass are found in a wide range of water bodies throughout their range, preferring cool, clear (meso-oligotrophic) lakes and streams with gravel or cobble substrates (Scott and Crossman 1973; Coble 1975). In the spring, smallmouth bass move from their overwintering grounds in deeper water into the shallow areas of lakes and rivers to spawn (Ridgeway et al. 1989). After spawning, females and subsequently males disperse to their preferred summer habitat of rocky areas in moderately shallow water (Scott and Crossman 1973). In streams, smallmouth bass have shown preference for slow (velocities between 10 and 50 cm/s), deep (>

60 cm) pools adjacent to boulders and logs, i.e., areas of reduced water velocities (Todd and Rabeni 1989). Sabo et al. (1996) noted that age-0 smallmouth bass occupied shallower habitats with higher velocities later in the summer and individuals using these habitats significantly improved their foraging success and first year growth. Once temperatures drop below 15°C in the fall, activity begins to decrease and they migrate to areas devoid of current for the winter months (Munther 1970; Langhurst and Schoenike 1990). Smallmouth bass, like most centrarchids, overwinter in water that is deeper and slower-moving relative to their summer habitat (Suski and Ridgeway 2009). In rivers, they are found in pools > 1.5 meters deep (Munther 1970; Bunt et al. 2002) and may migrate great distances in order to locate suitable habitat (Langhurst and Schoenike 1990).

Spawning takes place in late May or early June, when the water temperatures approach 15°C to 18°C (Turner and MacCrimmon 1970; Curry et al. 2005). Substrate preference includes areas dominated by cobble or gravel with no aquatic vegetation, although sites are often located near isolated boulders, logs, or dock pilings (Pflug and Pauley 1984). Large fluctuations in water levels can affect reproductive success (Montgomery et al. 1980). In streams, smallmouth bass seek out shallow, low velocity pools, often downstream of obstructions and with abundant overhead cover to construct their nest (Cleary 1956). Males create an oval shaped nest in gravel or cobble substrate (Saunders et al. 2002), in which one or more females deposit eggs. There is considerable pre-spawning activity by both the male and female fish (Ridgeway et al. 1989). Once eggs are deposited in the nest, the male guards the embryos and swim-up fry at this nest site until the fry disperse (Scott and Crossman 1973). Typical of all centrarchids, male smallmouth bass provide sole parental care for developing offspring (Breder 1936). In Oromocto and Mactaquac lakes (NB), embryos had hatched and fry were present as early as the end of May (Hanson and Curry 2005). In Second Lake (NS), spawning occurred during the first week of June, with fry present by the third week of June (McNeil 1995).

Smallmouth bass leave their overwintering areas and begin to feed when water temperatures reach 9 – 10° C. They are ravenous feeders during the pre-spawn period (Bain 1993), but feed very little during and after the spawning period while females recover and the males guard the nests. Supplemental feeding by guarding males has been documented and found to increase male survival and reproductive success (Ridgeway and Shuter 1994). In northern bass populations, Wiegmann and Baylis (1995) reported that male mortality following first reproduction may reach 94% due to starvation. Smallmouth bass undergo diet shifts during their life history. These shifts are size-dependent because smallmouth bass are gape-limited predators. A shift from small invertebrates to fish prey usually occurs later in the first year of life when smallmouth bass are 40 - 80 mm in length (total) (Hanson and Curry 2004). The timing of the shift to piscivory strongly influences growth, and subsequent survival and recruitment (Oliver et al. 1979). It is generally accepted that a rapid shift to piscivory results in higher growth rates and increased survival through the critical first overwinter period. Important prey are cyprinids (minnows), anadromous gaspereau (*Alosa* sp.), yellow perch (*Perca flavescens*), and crayfish (Keating 1970; Scott and Crossman 1973). In general, their diet is influenced by prey abundance and availability e.g., crayfish can compose more than 80% of the diet for individuals larger than 100 mm (Keating 1970).

Smallmouth bass growth is generally temperature-limited in the Maritimes as the species is at the northern limit of its distribution (McNeil 1995). Growth can be faster in lakes and reservoirs than in rivers because of generally warmer temperatures (Robbins and MacCrimmon 1974). In the warmer waters of southeastern Texas, smallmouth bass average 323 mm at age 5+ (Coble 1975). In Grand Lake (NS), age 5+ bass averaged 254 mm and in Elliot Lake (NS) the oldest

bass captured was age 9+ and 258 mm. In Skiff Lake (NB), bass reached 300 mm at age 7+, whereas in Harvey Lake (NB), bass reached 300 mm at age 5+ (Vickers 1998).

Achieving a minimum body size is critical for their first winter survival (Shuter et al. 1980) and it appears that 50 mm is the minimum in north-eastern waters, although the minimum size also appears to be depend on lake-specific variability (Curry et al. 2005). Growth appears to be density dependent for smallmouth bass (Gillooly et al. 2000) such that the high density in Elliot Lake (254/ha) probably contributed to relatively slow growth. Small adult body sizes are also found in lakes that contain other predatory fish species (Dunlop and Shuter 2006), which may explain the slower growth in Skiff Lake.

2.3 Smallmouth Bass Introductions and Invasion Effects

The introduction of a top piscivore like smallmouth bass can affect native fish communities through elimination of predation-intolerant species (Tonn and Magnuson 1982), restricting distribution of native species to complex habitats (MacRae and Jackson 2001), and competition for shared resources (Morbey et al. 2007). Reports on smallmouth bass introductions or invasions are dominated by observed impacts on lake ecosystems from nonindigenous waters of the Great Lakes region. Introductions often result in shifts in forage fish assemblages resulting from declines in abundance and decreases in diversity (Findlay et al. 2000; MacRae and Jackson 2001; Woodford et al. 2005). Salmonids can be impacted. Shifts in lake trout (*Salvelinus namaycush*) habitat use and trophic status and thus growth rates (Vander Zanden et al. 1999), and regional declines in brook trout (*Salvelinus fontinalis*) as well as other native piscivores (e.g., chain pickerel (*Esox niger*) and yellow perch) have been associated with smallmouth bass introductions (see Warner 2005 for a review). It is not discussed specifically, but a study of the trophic structure of the fish community downstream of the Mactaquac Dam on the Saint John River (at Fredericton, NB) indicates a very high probability that Atlantic salmon smolts and juveniles are an important component of smallmouth bass diets (Curry et al. 2007).

Attempts to demonstrate that introductions of smallmouth bass have actually caused or contributed to the decline of Pacific salmonids have been difficult (Fletcher 1991). The effects on salmonid populations have been studied extensively in western North America, primarily in the Columbia River Basin, where Pacific salmon populations have plummeted from an estimated 8 to 16 million to an average of <1 million (Nehlsen et al. 1991). Although dams are a major factor in the decline of salmon stocks, the introduction of invasive species such as smallmouth bass are considered to be a major contributor to the decline of Pacific salmon and other native fish populations (Bennett et al. 1991; Poe et al. 1991; Tabor et al. 1993; Zimmerman and Parker 1995). In contrast, smallmouth bass are sometimes reported to have minimal impact on Pacific salmon populations (Keating 1970; Reiman et al. 1991; Shrader and Gray 1999; Zimmerman and Ward 1999; Fayram and Sibley 2000; McElwee 2001; Summers and Daily 2001; Fritts and Pearson 2004). Juvenile salmonids were not a major component of smallmouth bass diets in the Lower Granite River (Naughton et al. 2004) or the John Day reservoir of the Columbia River (Shrader and Gray 1999; Fritts and Pearson 2004). Of an estimated 2.7 million juvenile salmonids consumed annually by predatory fishes in the John Day Reservoir, approximately 9% was attributed to smallmouth bass (Reiman et al. 1991). Northern pikeminnow (*Ptychocheilus oregonensis*), a native species, consumed 78% of the juvenile salmonids (Poe et al. 1991). Walleye, also an invasive species are estimated to consume 2 million salmon smolts annually in the Columbia River, or ~1/3 of total predation loss (McMahon and Bennett 1996). In Lake Washington, smallmouth bass appeared to have little impact on sockeye salmon (*Oncorhynchus nerka*) populations (Fayram and Sibley 2000).

Other studies have found that smallmouth bass appear to be important in determining survival of native cutthroat trout (*Oncorhynchus clarki*) in Lake Washington (Nowak et al. 2004) and the survival of out-migrating chinook salmon (*Oncorhynchus tshawytscha*) smolts (Tabor et al. 1993; Fresh et al. 2003; Fritts and Pearson 2004). Fritts and Pearson (2004) attributed the low survival of naturally produced, ocean-type chinook salmon in the lower Yakima River to predation by smallmouth bass. However, they found no evidence of significant predation on wild or hatchery stream-type chinook salmon, hatchery coho salmon (*Oncorhynchus kisutch*), or wild steelhead trout (*Oncorhynchus mykiss*). Juvenile chinook salmon composed >50% by weight of smallmouth bass diets in the Columbia River (Tabor et al. 1993) and Lake Washington (Fresh et al. 2003).

3.0 ATLANTIC SALMON

3.1 Historical and Current Distribution

In North America, Atlantic salmon ranged historically from Ungava Bay in northern Quebec southward along the Atlantic coast to the Connecticut River (Connecticut). Their range also extended westward into Lake Ontario, Lake Champlain, and the Finger Lakes (Scott and Crossman 1973; Webster 1982). At one time, 875 rivers had healthy populations of wild Atlantic salmon; currently, that number is 747 rivers and population sizes are reduced in all rivers (AFS 2009). In Canada, sustainable, reproducing populations remain throughout most of the historic range. However, 28 rivers in the United States appear to have lost all naturally reproducing populations and the Gulf of Maine Distinct Population Segment has been declared endangered (NRC 2003). Only eight rivers in Maine currently support wild Atlantic salmon populations, with the largest population occurring in the Penobscot River. Stocking of hatchery-reared fish has maintained salmon in Maine rivers (Fay et al. 2006).

New Brunswick's salmon rivers are dominated by three large and complex watersheds - the Saint John, Miramichi and the Restigouche. There are >100 other rivers that support wild populations. All rivers of the inner Bay of Fundy have critically low population sizes and 32 populations have been declared endangered (10 populations are in NB). Other rivers draining into the Bay of Fundy (e.g., Saint John, Magaguadavic, and St. Croix Rivers), have seen a critical decline in numbers since 1990 (AFS 2009). Gulf of St. Lawrence rivers have greater production of Atlantic salmon. The Miramichi River alone is capable of producing more Atlantic salmon than any other river in North America (Chaput 1995). The Restigouche is noted for its large salmon which spend multiple years at sea before returning to spawn (Chaput et al. 2006).

3.2 Life History

Atlantic salmon are typically anadromous, using rivers for reproduction and juvenile development and the marine environment for adult development and rapid growth (Mills 1989). Throughout early life in freshwater, each stage from newly emerged fry to smolt may use different habitats. The principal determinants of habitat suitability are water depth, velocity, stream bed substrate, cover, and temperature (Heggenes 1990). Optimal microhabitat is considered to be areas where velocity is low but is associated with nearby faster velocities. In these areas, the availability of drifting invertebrates is high, but the energy required to maintain their position is relatively low (Nislow et al. 1999, 2000). As water temperatures drop below 9°C, fish move to deeper water or under cover such as boulders where they remain during winter and reappear in spring when temperatures reach 6 to 7°C (Rimmer et al. 1983; Rimmer 1984). Feeding continues throughout the winter, with most activity occurring between dusk and dawn

(Cunjak 1988). Atlantic salmon often select overwintering sites near high velocities, which reduces sedimentation (Cunjak 1988), and will sometimes occupy these fast riffles (S. Coghlan, unpublished data).

Salmon spawn in autumn or early winter when water temperatures are $<6^{\circ}\text{C}$ (Decola 1970). Females dig nests (redds) in which eggs are deposited and fertilized by one or more males. Embryos incubate over winter, hatch in the substrate, and emerge as free-swimming alevins (fry) in late spring or early summer. This development period is temperature dependent. When they emerge from the substrate, they are approximately 30 - 40 mm in length and begin exogenous feeding on invertebrate prey (Dill 1977). The fry are referred to as age 0+ juvenile or young-of-the-year and will grow to about < 70 mm or less by the end of the first summer of life (Baum 1997; Swansberg et al. 2002). Natural mortality is highest during the early free-swimming period (see review in Bley 1987).

In the parr's second or third spring (generally when body size reached 100 - 150 mm), physiological changes occur that result in visible morphological and behavioural characteristics, i.e., smoltification, which prepares the salmon for migration to and survival in a marine environment (Hoar 1976). In the Miramichi River, NB, the majority of smolts emigrate at age 2+ or 3+ (Cunjak 1995; Chaput et al. 2006), however, smoltification can occur in their 5th year in freshwater. In general, there is a negative correlation between average river temperature (latitude) and age of smolts (Chaput et al. 2006). Whereas some smolts begin downstream migration in the fall, the majority migrate downstream in spring when water temperatures are $>5^{\circ}\text{C}$ (Jonsson and Ruud-Hansen 1985). They tend to travel near the water surface and at night (e.g., Bley 1987; Moore et al. 1995). Smolts in the Penobscot River (ME) began emigrating after water temperatures reached 5° C and are in full migration at 9 - 10° C (McCleave 1978). Most of the smolts (89%) in the Magaguadavic River (NB) were captured over a 29 day period in 2002 when water temperatures averaged 13.9° C (Carr et al. 2004).

After emerging from spawning gravel in the early spring, Atlantic salmon fry migrate to shallow, low-velocity habitats and near the bank margins, and feed on zooplankton, midge larvae, and other small invertebrates (Williams 1981). These habitats are especially energetically-profitable for small fish with limited swimming- and prey-capturing abilities during periods of cold temperatures and high discharges associated with spring runoff (Nislow et al. 2000). As the season progresses, stream water warms, and stream flows subside, there is a concomitant increase in body size, metabolic rate, swimming ability, and consumptive capacity of these fry. When they are several months old, the fry develop very noticeable markings along their flanks. They are then termed salmon parr. As a result of changing habitat profitability, parr move into faster and deeper habitats, and select and defend feeding locations from which they can maintain refuge from swift currents while at the same time intercept drifting invertebrates (Wankowski and Thorpe 1979; Smith and Li 1983; Hayes et al. 2000). Social hierarchies form in which dominant individuals maintain the most profitable feeding stations and exclude subordinates (Jenkins 1969; Wankowski and Thorpe 1979). However, by mid-summer, stream discharge and availability of aquatic prey often are reduced, such that the opportunities for energy gain diminish while energetic requirements increase, thereby forcing parr to occupy the swiftest habitats available. Although additional energy is expended while swimming against swift currents, increases in metabolic scope and prey delivery rates may allow compensatory energy intake in these habitats (Smith and Li 1983); if not, starvation and weight loss occur (Li and Brocksen 1977). During the most energetically-challenging periods (mid-summer), terrestrial invertebrates falling into the stream from adjacent riparian zones become an extremely important energy subsidy to Atlantic salmon (Johansen et al. 2005) and other salmonids (Kawaguchi and Nakano 2001; Sweka and Hartman 2008), triggering changes in foraging

behaviour and habitat use (Nakano et al. 1999; Baxter et al. 2004). When at sea, salmon eat a variety of marine organisms including zooplankton, but typically select fish and larger crustaceans (Hislop and Shelton 1993). Once adult salmon have returned to their natal river from the sea, they will migrate upstream from June to November holding in deeper, coolwater pools for various periods. Their migration patterns depend on water levels and temperatures in the river (Fleming 1996).

4.0 THE INTERSPECIFIC INTERACTIONS: KNOWN AND POTENTIAL

Smallmouth bass can exert very strong influences on the structure of littoral zone fish communities (MacRae and Jackson 2001). Because of their voracious feeding habits and spatial and temporal habitat use that overlaps with Atlantic salmon, negative impacts on Atlantic salmon are expected (Meister 1982; Fay et al. 2006). However, little empirical data exists to test confirm this hypothesis. van den Ende (1993) investigated the food habits of chain pickerel and smallmouth bass in the Penobscot River (ME) to determine the importance of smolts in their diets. No smolts were found in any of the smallmouth bass stomachs sampled. Smallmouth bass were not considered significant predators of Atlantic salmon due to large salmonid size, habitat use, as well as physiological constraints of water temperature on smallmouth bass feeding (van den Ende 1993; Tabor et al. 1993). Unfortunately at present, there are no direct studies of interactions of smallmouth bass and Atlantic salmon

4.1 Predation Potential

Predation risk depends in part on the degree of overlap of predator-prey habits and habitats in time and space (Hampton 2004). Anthony (1994) and Mather (1998) provided a review of Atlantic salmon predators and the sensitivity of each life stage to predation. Predation on eggs and alevins is not normally an important source of mortality as these stages are buried within the substrate, although Atlantic salmon parr and brook trout are known to feed on the eggs (White 1939). Fry and parr may be preyed upon by various piscivorous fish including brown trout (*Salmo trutta*) and brook trout, chubs (*Semotilus* sp.), slimy sculpin (*Cottus cognatus*), burbot (*Lota lota*), northern pike (*Esox lucius*), chain pickerel, largemouth bass, smallmouth bass, and yellow perch (MacCrimmon 1954; Warner et al. 1968; Mills 1964; Baum 1997; Henderson and Letcher 2003; Ward et al. 2008). In rivers, juvenile Atlantic salmon prefer shallow, fast-flowing water with a moderately coarse substrate with cover, generally avoiding deep or slow-moving water (Baglinière and Champigneulle 1986) although larger parr will select deeper pools (Bremset and Berg 1997). Smallmouth bass avoid strong currents and larger individuals prefer deeper pools (Rankin 1986; Edwards et al. 1983). However, age 0+ smallmouth bass will select less preferred shallower riffle habitats to access a greater range of invertebrate prey (Sabo et al. 1996), which may increase overlap with Atlantic salmon. Bonar et al. (2005) found that predation on Pacific salmon by largemouth bass was greatest in small lakes with large littoral zones. Larger lakes and rivers offer greater spatial separation of bass and salmon (Bjornn and Piaskowski 1999).

The smolt stage is considered a vulnerable stage because their migration to sea may increase spatial and temporal overlap with predators (McCormick et al. 1998). In most systems, the high aggregation of smolts swamp predators, however, if overlap does occur, predators can aggregate downstream to prey on out-migrating smolts (Mather 1998). Smolts can be preyed upon by brook trout, chain pickerel, smallmouth bass, striped bass (*Morone saxatilis*), and northern pike (van den Ende 1993; Moring et al. 1999; Jepsen et al. 1998; Mohler et al. 2002; Beland et al. 2001). Juvenile salmonids have strong anti-predator behaviour in the presence of

smallmouth bass (van den Ende 1993). Controlled experiments demonstrated that smolts were often able to escape attack. The smolts struggled violently and could only be consumed if captured from the anterior end.

Significant predation by smallmouth bass on out-migrating Pacific salmon smolts has been documented (Fresh et al. 2003; Fritts and Pearson 2004; Tabor et al. 2007). In Lake Washington, salmonids were found in smallmouth bass stomachs only during the out-migration, when smolts were concentrated in the littoral zone (Fayram and Sibley 2000). Smallmouth bass congregate in large numbers along the Lower Yakima River in spring, coinciding with the downstream migration of chinook salmon. Smallmouth bass are the most abundant piscivore in the lower Snake River reservoir (Washington) and in spring, ~35,000 smallmouth bass move from the reservoir into the river to feed on migrating smolts (Zimmerman and Parker 1995; Pearson et al. 1999).

Migrating smolts may be temporally segregated from smallmouth bass because migration generally occurs at night (Thorpe and Morgan 1978), whereas smallmouth bass are primarily crepuscular feeders (Todd and Rabeni 1989). In Lake Washington, low predation on migrating salmon in May and June was attributed to low water temperatures (< 15° C). Some degree of spatial segregation in spring may also occur because smolts migrate in the main river channel, while bass are spawning in shallow, backwater areas. Areas of high flow will displace smallmouth bass eggs and fry (Scott and Crossman 1973; Lorantas and Kristine 2004). However, smallmouth bass also require areas of cobble or gravel substrate and adequate water depth which is often found in the main channel of rivers (Saunders et al. 2002; Lorantas and Kristine 2004). Insects often comprise a large proportion of smallmouth bass diet in the spring, most likely the result of a high availability of emerging insects at this time (van den Ende 1993; Dauwalter and Fisher 2008). If present, crayfish become a large proportion of smallmouth bass diet in spring, even with migrating salmon smolts present (Fayram and Sibley 2000). Fritts and Pearson (2004) found that smallmouth bass decreased consumption of chinook salmon in June, switching to a diet composed of higher percentage of invertebrates and crayfish, despite the continued availability of smolts. In part, smallmouth bass may prefer insects and crayfish because they are easier to capture and offer the best energy return on investment rather than actively searching out larger prey.

Smolts probably have lower risk of predation than younger fry and parr owing to the larger body size of smolts. Fritts and Pearson (2006) reported that smallmouth bass generally prey on Pacific salmon that averaged 25% of predator length. Arndt's (1996) survey of spawning smallmouth bass in NB waters reported male body lengths of 200 to 480 mm; thus maximum prey size for mature individuals is predicted to be 50 to 120 mm and smaller for immature smallmouth bass. Vickers (1998) predicted that the maximum body depth of forage fish a standard 300 mm smallmouth bass could consume was 31.2 mm. Atlantic salmon body depth is approximately 20% of the total length (Danie et al. 1984), therefore, a 300 mm smallmouth bass would be able to ingest smolts up to 150 mm in size. Atlantic salmon smolts are on average >100 mm, e.g., migrating smolts in the Northwest Miramichi River (NB) range from 105 to 240 mm in length (Chaput et al. 2002).

Adult Atlantic salmon migrating upriver in summer and fall prefer deep and cool pool habitats where they can hold outside the main current of the river. These deeper, lower velocity areas in a river are similarly the preferred habitats of larger smallmouth bass. However, Atlantic salmon returning from the sea are typically >500 mm in body length which surpasses the gape limitation of the average-sized, adult smallmouth bass (Fritts and Pearson 2006).

4.2 Competition

Interspecific competition in the wild can be difficult to detect because coexisting species have evolved behaviours to minimize any niche overlap (Bergman and Greenberg 1994). Such niche-partitioning mechanisms are commonly seen between co-evolved species, such as Atlantic salmon and brook trout in eastern rivers (Gibson 1973). When coexisting, the two species segregate such that Atlantic salmon occupy relatively shallow, fast habitats, whereas brook trout occupy relatively slow, deep habitats (Gibson 1973), although this pattern may vary depending on age and size of fish (Sayers 1990) and density (Bult et al. 1999). Presumably, interspecific differences in habitat selection, enabled by differences in physiology and morphology (e.g., larger, more hydrodynamic pectoral fins in Atlantic salmon; Arnold et al. 1991), have been selected during the co-evolutionary process and thus minimize competition for foraging habitats. There are many other examples of such niche partitioning among co-evolved salmonids (Fausch et al. 1997; Nakano et al. 1999; Miyasaka et al. 2003; Hasegawa and Maekawa 2006). However, when an exotic top predator is introduced into an aquatic ecosystem, impacts can be devastating particularly in less complex systems because competition potential is focused on fewer species and habitats. Also, because native salmonids and invasive fish do not share a co-evolutionary history and have not experienced selective pressures to evolve niche-partitioning mechanisms, the resulting competitive interactions may be intense. Native lake trout populations can be restructured when smallmouth bass are introduced as smallmouth bass may out-compete lake trout for forage fish in profitable littoral habitats (Vander Zanden et al. 1999; Jackson 2002; Morbey et al. 2007). There are reported correlations between smallmouth bass invasions and altered fish communities (as discussed), however, the extent of competition with Atlantic salmon in eastern rivers is unknown. However, based on examples of competition between Atlantic salmon and various co-evolved and non-native species, we can make predictions.

A recent study undertaken at the University of Maine (R. Wathen and S. Coghlan, unpublished data) has found evidence of competition between smallmouth bass and Atlantic salmon in artificial habitats. Age-0 smallmouth bass can alter their microhabitat use throughout the course of development, using not only the pool habitats where they were spawned but also moving into shallower areas associated with riffles (Sabo and Orth 1994). In artificial stream channels, the introduction of smallmouth bass was found to increase the movement rates of Atlantic salmon and decrease the duration of residency in any particular location (R. Wathen and S. Coghlan, unpublished data). In the absence of smallmouth bass, Atlantic salmon remained relatively sedentary and selected heads of pool habitat type. In a controlled-invasion experiment, six stretches (25-m long) of stream were isolated. All resident fish (including age 0+ Atlantic salmon) were removed and were reintroduced into all reaches at a constant density. After snorkeling and measuring habitat use (depth, velocity, substrate, distance to nearest neighbour), age 1+ smallmouth bass were introduced into half the sites, more juvenile salmon into the remaining sites, and the snorkeling survey was repeated. Habitat use was highly variable and did not appear to depend on the presence of smallmouth bass, but detectability of the salmon was reduced by 50% when smallmouth bass were present, probably because the salmon adopted hiding behaviours. In a second field study (R. Wathen and S. Coghlan, unpublished data), a range of streams that contained age 0+ salmon only, age 0+ smallmouth bass only, and salmon and smallmouth bass in sympatry, were selected and monitored for habitat use (by snorkelling) throughout the summer. For a brief period during late summer, both species overlapped significantly in habitat use (in riffles) when in sympatry, but smallmouth bass moved into deeper, slower water by the fall. There is some evidence that Atlantic salmon parr will overwinter in pools (Whalen and Parrish 1999; Mäki-Petäys et al. 2004) which would found that riffle habitat is most utilized by overwintering salmon (Rimmer et al. 1983; Cunjak 1988;

Roussel et al. 2004; Stickler 2008). From these field studies, it seems that competition is most likely to occur between age 0+ individuals of both species, but probably only for a brief period of time in the late summer.

Furthermore, any innate habitat partitioning mechanisms between native Atlantic salmon and brook trout could break down upon invasion of smallmouth bass. This would be similar to the findings of Hasegawa and Maekawa (2006) that competition between two native, co-evolved salmonids occurred only in the presence of a third, exotic species. If age 0+ smallmouth bass force age 0+ salmon from riffles into pools, the parr may be more vulnerable to predation by brook trout. If juvenile and adult smallmouth bass force brook trout from preferred pools into riffles and runs, the trout may be forced to compete with salmon juveniles. Most likely, negative effects on both Atlantic salmon and brook trout resultant from competition with smallmouth bass would be most pronounced during energetically-stressful summer periods of high water temperatures, reduced stream flows, and decreased prey availability. Under such conditions, smallmouth bass should be the energetically-favoured species and thus emerge as the competitive superior. Changes in landscape- or climate-related variables that cascade to alter in-stream habitat may exacerbate the invasion, establishment, and ultimately competitive impact of smallmouth bass in native salmonid streams.

4.3 Summary of Interactions

When smallmouth bass are introduced into a water body, they prey heavily on smaller fish. In eastern rivers, this would be a limited diversity of small-bodied cyprinid species (e.g., blacknose dace (*Rhinichthys atratulus*) and creek chub (*Semotilus atromaculatus*) and the slimy sculpin (*Cottus cognatus*)), juveniles of larger non-salmonids (e.g., white sucker (*Catostomus commersonii*), white perch (*Morone americana*), and anadromous gaspereau (alewife – *Alosa pseudoharengus* and blue-back herring – *Alosa aestivalis*)), juvenile brook trout and Atlantic salmon (Danehy 1984; Weidel et al. 2000; Hanson and Curry 2005; Weidel et al. 2007). The predation risk leading to the most significant potential threat to Atlantic salmon will be consumption of juveniles (emerging fry to smolts) by smallmouth bass of all ages. The potential for direct competitive interactions between juvenile smallmouth bass and Atlantic salmon in streams has not been demonstrated, but is likely. Studies of habitat use and foraging behaviour of juvenile smallmouth bass in streams (Sabo et al. 1996) suggest functional similarities and potential habitat overlap with Atlantic salmon that could result in competitive interactions. For example, Sabo and Orth (1994) and Sabo et al. (1996) found that age 0+ smallmouth bass spend a portion of their first summer in shallow areas associated with riffles and runs, i.e., when individuals are > 30mm in length, which is believed to increase access to a greater range of invertebrate prey via drift-foraging. The most energetically-profitable foraging habitats for age 0+ smallmouth bass are characterized by depths less than 60 cm and velocities between 10 cm and 50 cm/s, which is almost identical to optimal habitat for age 0+ Atlantic salmon (Nislow et al. 1999). During mid-summer, terrestrial invertebrates falling into streams from adjacent riparian zones become an important energy resource for juvenile Atlantic salmon (Johansen et al. 2005) and this stream side resource is entering in preferred smallmouth bass habitat. Overlying both predation and completion potential is the smallmouth bass's preference of warmer water and lower water velocities than Atlantic salmon. This suggests the period of maximum interaction will be mid to late summer in eastern rivers when water levels are low, concentrating fishes, and warmer temperatures maximize the thermal stress on Atlantic salmon.

4.4 Water Temperature and Climate Change

It would be predicted that the general coldwater intolerance of smallmouth bass can restrict interaction with Atlantic salmon during some periods of the year. Fayram and Sibley (2000) hypothesized that the low predation on sockeye salmon fry was a result of low temperatures which physiologically limited feeding by smallmouth bass. Salmon smolts avoided predation by smallmouth bass if their migration was initiated before water temperatures warmed in spring (Fresh et al. 2003). Coincidentally, water temperatures during the open water season are slowly rising in eastern rivers (Haro et al. 2009). A warmer river environment implies increasing potential for interactions between sympatric smallmouth bass and Atlantic salmon with the former increasing feeding to meet higher metabolic demands (Rogers and Burley 1991) and the latter suffering increasing thermal stress.

Swansberg et al. (2002) examined the relations between climate, hydrological parameters, and the fork length of juvenile salmon in the Miramichi River (NB). Fork length of juvenile salmon parr was found to have declined significantly during the period of warming observed over the time period studied. This trend suggests future climate change will reduce growth rates of juvenile Atlantic salmon and thus potentially increasing their susceptibility to a gape limited predator such as the smallmouth bass. Increasing water temperatures are predicted to cause ecological shifts reducing the ability of salmonids to compete with warm water species (McCollough 1999). For example, Taniguchi et al. (1998) showed that the competitively-dominant species changed from brook trout to brown trout to creek chub as stream temperatures increased from 18°C to 26°C. Coghlan and Ringle (2005) presented field and laboratory data suggesting that in the presence of exotic rainbow trout, the competitive ability of Atlantic salmon parr decreased as temperatures increased from 15°C to 25°C. Optimal temperatures for growth and energetic return on investment range from 16°C to 19°C for Atlantic salmon (Murphy 2003) and from 22°C to 24°C for smallmouth bass (Sabo et al. 1996). If we expect each species to be competitively-dominant closer to its optimal temperature, then anticipated climatic warming should increasingly favour smallmouth bass at the expense of Atlantic salmon.

5.0 CONCLUSION

The movement of species beyond their native range is recognized as one of the most ecologically damaging effects of human activities, threatening biodiversity and ecosystem health worldwide (Ricciardi and Rasmussen 1998). Smallmouth bass introductions or invasions have resulted in dramatic, adverse impacts on native species and ecosystems, but some introductions have little or no observed impact. This variability in degree of impact most probably relates to scale of interaction: competition and predation will be most significant when systems are less biologically and physically complex (i.e., low diversity communities and restricted habitats). In most eastern rivers inhabited by Atlantic salmon, both conditions are common. There are few fish species – the average species diversity in Maritime rivers <16 species (Curry 2009). Habitats for older smallmouth bass would be slow, deeper waters (i.e., pools), however, age-0 smallmouth bass have been shown to inhabit riffles during late summer. Consequently, a significant degree of interaction between Atlantic salmon and smallmouth bass is predicted to occur in eastern rivers. The degree of interaction is also predicted to increase as a consequence of increasing summer temperatures in rivers resulting from global warming.

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